THE LARVA OF NEOTROPICAL *ENCELADUS GIGAS* BONELLI (COLEOPTERA: CARABIDAE: SIAGONINAE: ENCELADINI) WITH NOTES ON THE PHYLOGENY AND CLASSIFICATION OF SOME OF THE MORE PRIMITIVE TRIBES OF GROUND BEETLES

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ABSTRACT

The third instar larva of *Enceladus gigas* Bonelli is described and illustrated. Its relationship with *Siagona* (Siagonini) is discussed. Both larval and adult structural features indicate clear relationship between the two groups, yet at the same time show enough divergence to support tribal ranking for both with our present concept of that category. Structural features of the mesotibia of members of the following taxa are discussed: Amphizoidae, Apotomini, Bembidiini, Brachinini, Carabini, Cicindelinae, Crepidogastrini, Cychrini, Cymbionotini, Elaphrini, Enceladini, Hiletini, Loricerini, Melaenini, Metriini, Migadopini, Nebriini, Omophronini, Opisthiini, Ozaenini, Patrobini, Promecognathini, Psydrini, Scaritini, Siagonini, Trechini. The distribution of these mesotibial characteristics is given and the potential impact on our knowledge of carabid phylogeny is noted, although formal changes in classification are not made at this time; except that *Cymbionotum,* formerly regarded as the single genus of Cymbionotini is here included in the Siagonini.

INTRODUCTION

The largest and one of the least known Neotropical ground beetles is *Enceladus gigas* Bonelli. This monotypic genus has been regarded as the single member of Enceladini since Horn (1881) erected the tribe. Lacordaire (1854), followed by Chaudoir (1876), was the first to place *Siagona, Luperca,* and *Enceladus* in Siagonini. Recent studies (Ball, Kavanaugh *in litt.)* also indicate a close relationship between *Enceladus* and members of Old World Siagonini, especially through some character states shared with *Luperca* species.

The larva of *Enceladus* described herein clearly indicates relationship with *Siagona,* but not a close one (Table II). The larva of *Siagona brunnipes* Dejean (Moore, 1972) has numerous apotypic features and must be considered highly derived, whereas that of *Enceladus* is much more conservatively derived from the "normal" carabid larva type. This fact, and consideration of adult structural features (e.g. body form, antennal cleaner), indicate that *Enceladus* is an old relict lineage on the periphery of the range of the group. Its survival was probably enhanced by rifting of African and South America in the Mesozoic.

The present distributions of the members of the 4 genera under consideration here (Table I) indicate old relict patterns, separation of major taxa for millions of years, and certainly enough time for major divergent radiation and extinction.

Table I

Distribution of Taxa of the Subfamily Siagoninae

Taxon	Distribution
Enceladini	
Enceladus	New World mid-tropics; Venezuela, Trinidad, and Brazil
Siagonini	
Luperca	Old World; India and Africa
Cymbionotum	Old World; southern Palaearctic, southern Asia but not Malay Archipelago, Africa
Siagona	Old World; south Palaearctic, southern Asia including Malay Archipelago, Africa

Table II

Larval characters and character states of Enceladus gigas and Siagona brunnipes

Character	Taxon and Character States	
	Enceladus	Siagona (from Moore, 1972)
Mouthparts		
A. Mandibles		
dorsal surface	setigerous channel	asetose, no channel
retinaculum	short, stout, truncate	short, stout, sharp
molar area	setigerous	setigerous
scrobal area	asetose	asetose
penicillus	absent	absent
B. Maxilla		
terminal palpomere	short, broad, with disc-like sensilla	thread-like, long, no disc sensilla
inner lobe	short, stout, unisetose	large, stout, bisetose
outer lobe	2 equal articles	2 unequal articles
C. Ligula	absent	absent
Head		
D. Eyes	6 ocelli	1 ocellus
E. Antennae	(broken)	long, 4 articles, no 3rd article sensor, terminal antennomere whip-like
Legs		
F. Claws	2	2
Abdomen		
G. Chaetotaxy, dorsal	1+1, caudal edge	1+1, caudal edge
H. Urogomphi	multisegmented, long 1 seta	unsegmented, long plurisetose

It is my purpose here on the occasion of the larval description of *Enceladus gigas* to also offer a preliminary character state analysis of adult structure. The analysis shows that old classifications viewed with new study techniques and discovery of new character states of included taxa give insights into carabid relationships beyond those based on traditionally used character states.

Enceladus gigas Bonelli (Larva)

Third Instar Larva (Figs. 1, 2).—Length (anterior edge of nasale to apex of pygopod, specimen somewhat shrunken from poor preservation techniques) 43.0mm; width (across head) 7.5mm, width (across metanotum) 8.5mm.
Color. Head, mandibles, and caudal margin of each thoracic and abdominal tergum black, sides and fore-edge of abdominal terga piceous; mouthparts, legs, venter, urogomphi, and disc of segments rufous or rufotestaceous.
Form. Body and appendages markedly sclerotized throughout; robust, moderately depressed.
Chaetotaxy. Body setae few, located as follows—one near each hind angle of all terga, one near each hind angle of sterna I to VIII, one on hind edge of median pleurite I to VIII, pair at each hind angle of sternum XI; appendage setae few, located as follows—one medio-ventral each urogomphus, several each coxa and trochanter; head setae (Figs. 1, 2).
Head. (Figs. 1, 2). Large, square, hind angles rounded, neck broad. Surface rugose. Epicranial suture narrowly "V"-shaped with broadly arcuate anterior portion extended to base of mandible. Nasale a broadly truncate tooth with two small lateral tubercles. Frontoclypeal area concave. Antennae unknown (broken in specimen).
Mouthparts. (Figs. 1, 2). Mandibles large and robust with markedly arcuate form, each with large truncate retinaculum and setigerous molar area; dorsal channel setigerous throughout. Maxillae large and stout, densely setigerous medially; inner lobe a small tubercle with a single seta at apex; outer lobe with two articles of equal length, each with numerous setae on medial side; palp with four articles, the last with several large disc-like sensors. Ligula large and robust, densely setigerous dorsally and medially, without apical setae; palp with two articles, the last with several large disc-like sensors. Stemmata six each side of head, in two rows of three each side.
Spiracles. Prothoracic very large, elipsiform, unitextured; abdominal ones smaller, more spherical, bitextured.
Body. (Fig. 1). *Legs.* (Fig. 1). *Urogomphi.* (Fig. 1). Fixed on sternum IX; long and multisegmented, unisetigerous.
Material examined. "Brickfield, Trinidad, March 14-17, 1947, Trinidad Zool. Exped. F. Wonder coll." 1 specimen.

The above description is based on a single specimen discovered in the miscellaneous larval collections of the Field Museum of Natural History, Chicago, by John F. Lawrence, and I thank both him and Henry Dybas for forwarding the specimen to me. Its determination as *Enceladus gigas* was accomplished by a process of elimination. Its size precludes anything else. Subsequent study of it showed synapotypic character states with *Siagona* larvae.

Comparison with *Siagona brunnipes*

The larvae of *Enceladus* and *Siagona* share 3 important apotypic features. Both have extremely long urogomphi, unusual for the "primitive" carabid tribes and found elsewhere only in the advanced chlaeniines and galeritines. However, *Siagona* has lost external segmentation of these appendages and gained long setae throughout their length. Both larvae lack

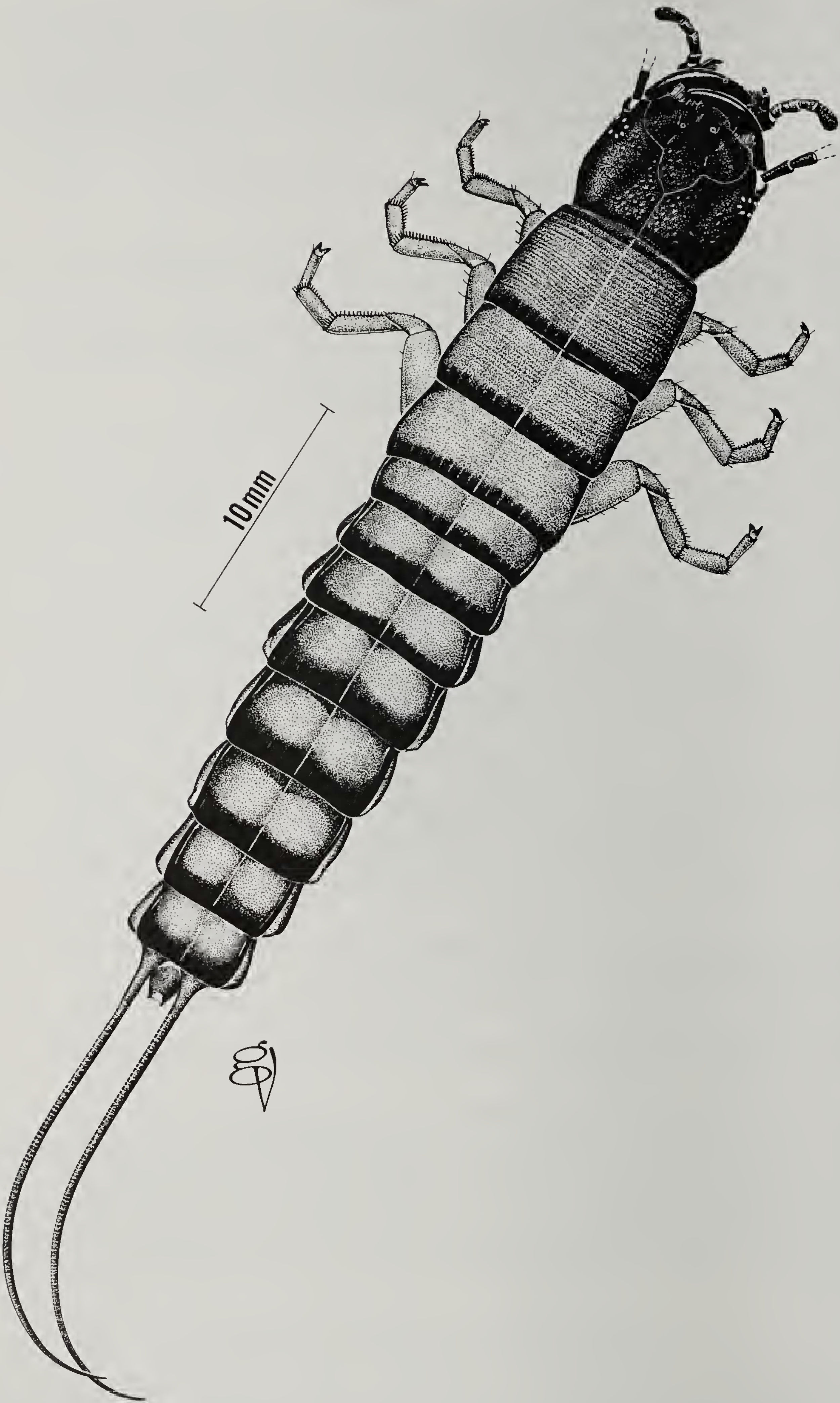

Fig. 1. *Enceladus gigas* larva, dorsal aspect, Brickfield, Trinidad.

a ligula. This structure is also missing in the free-living larvae of *Trachypachus* and *Gehringia* and from among some of the ectoparasitoid larvae, such as found in *Lebia* and Brachinini. The dorsal chaetotaxy, although presently poorly surveyed among carabid larvae, is identical in *Enceladus* and *Siagona* larvae. Less important perhaps is the fact that neither larvae has a penicillus nor "scrobal" seta. The latter feature is almost universally found throughout carabid larvae, and its absence is something to be

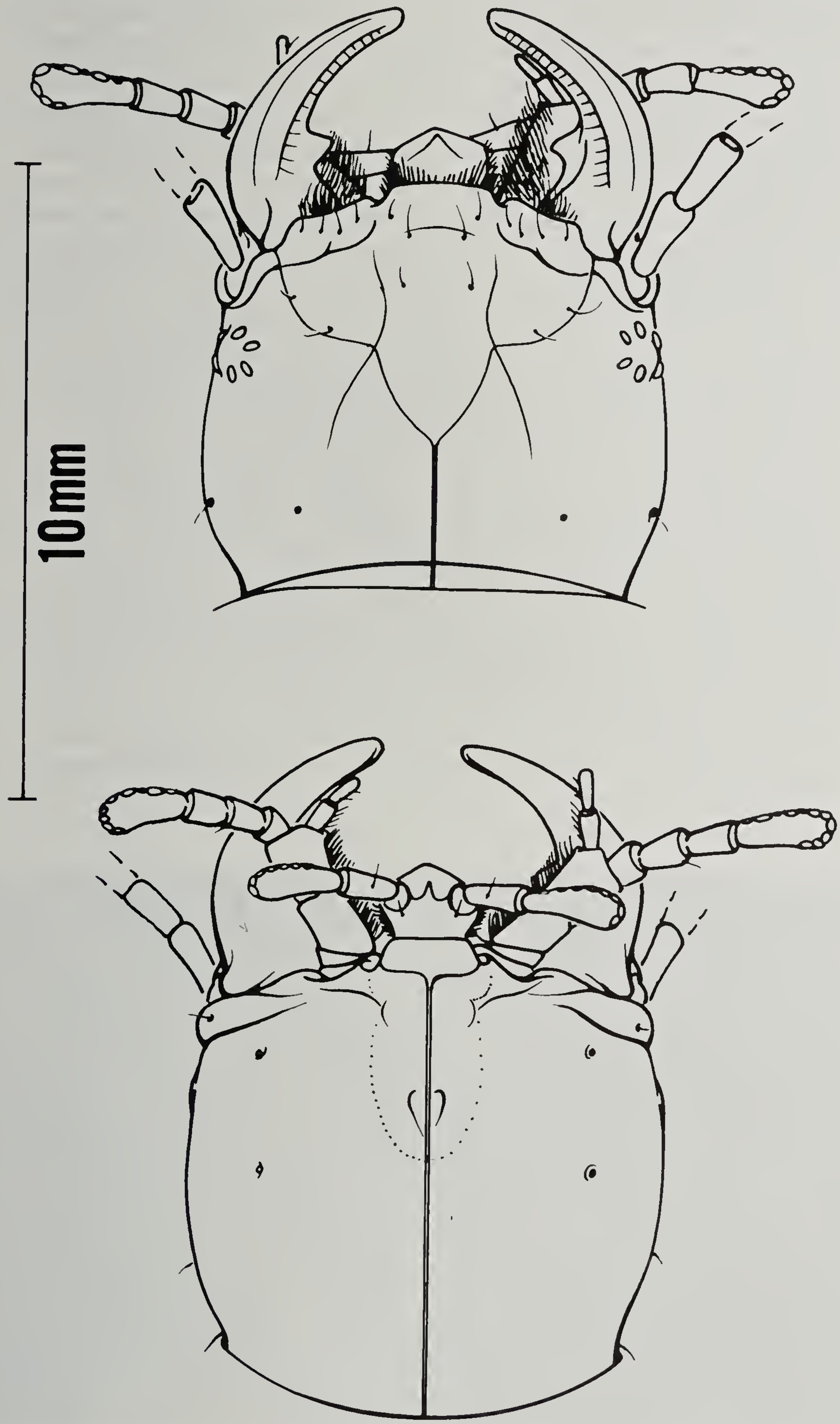

Fig. 2. *Enceladus gigas* larval head capsule, dorsal and ventral aspect, Brickfield, Trinidad.

noted. Unfortunately the antennae of the single *Enceladus* larva available are broken and cannot be compared to the unique *Siagona* antennae. Further study or discovery of larvae (e.g. Hiletini, *Cymbionotum, Luperca)* in other primitive carabids must be undertaken to show the relative apotypy of these character states.

Phylogenetic and Zoogeographic Considerations

A survey of the distribution of a mesotibial oblique comb (Fig. 4) indicates that several taxa heretofore generally unassociated should be considered as possibly related. The oblique comb characterizes adult members of Elaphrini, Promecognathini, Loricerini, Migadopini, Apotomini, and Melaenini (and see *Lissopterus,* below). A similar structure, still in need of careful analysis, exists in *Bembidion (Chrysobracteon)*; I suspect this is a case of convergence, however. The survey also showed that another mesotibial structure, a brush on the lateral surface (Fig. 3) exists in the following taxa: Cicindelinae, Amphizoidae, Hiletini, Carabini, Cychrini, Nebriini, Opisthiini, Enceladini, and Siagonini (+*Cymbionotum).* In addition, members of Metriini, Psydrini (*Nomius*), Notiophilini, Patrobini, and Omophronini have a more diffuse apical brush which may be derived or antecedent to the lateral brush. The migadopine, *Lissopterus,* possesses both the oblique comb and lateral brush. Metriini also have a medial surface mesotibial brush like that in Brachinini, Crepidogastrini, and Ozaenini. All the other "primitive" tribes (Broscini, Scaritini, Rhysodini, Trachypachini, Gehringini, Pseudomorphini, Trechini, Psydrini) were surveyed and found not to have these mesotibial features, although certain *Pasimachus* (Scaritini) have a close set row of setae on the lateral mesotibial surface which may or may not be homologous with the precursor to the brush. *Nomius* (Psydrini) has a very diffuse brush lateroapically.

Students of carabid higher classification may well find this set of character states useful in sorting out taxonomic ambiguities caused by convergent evolution of other states such as the antennal comb, open procoxal cavities, and elytral interneur number and condition.

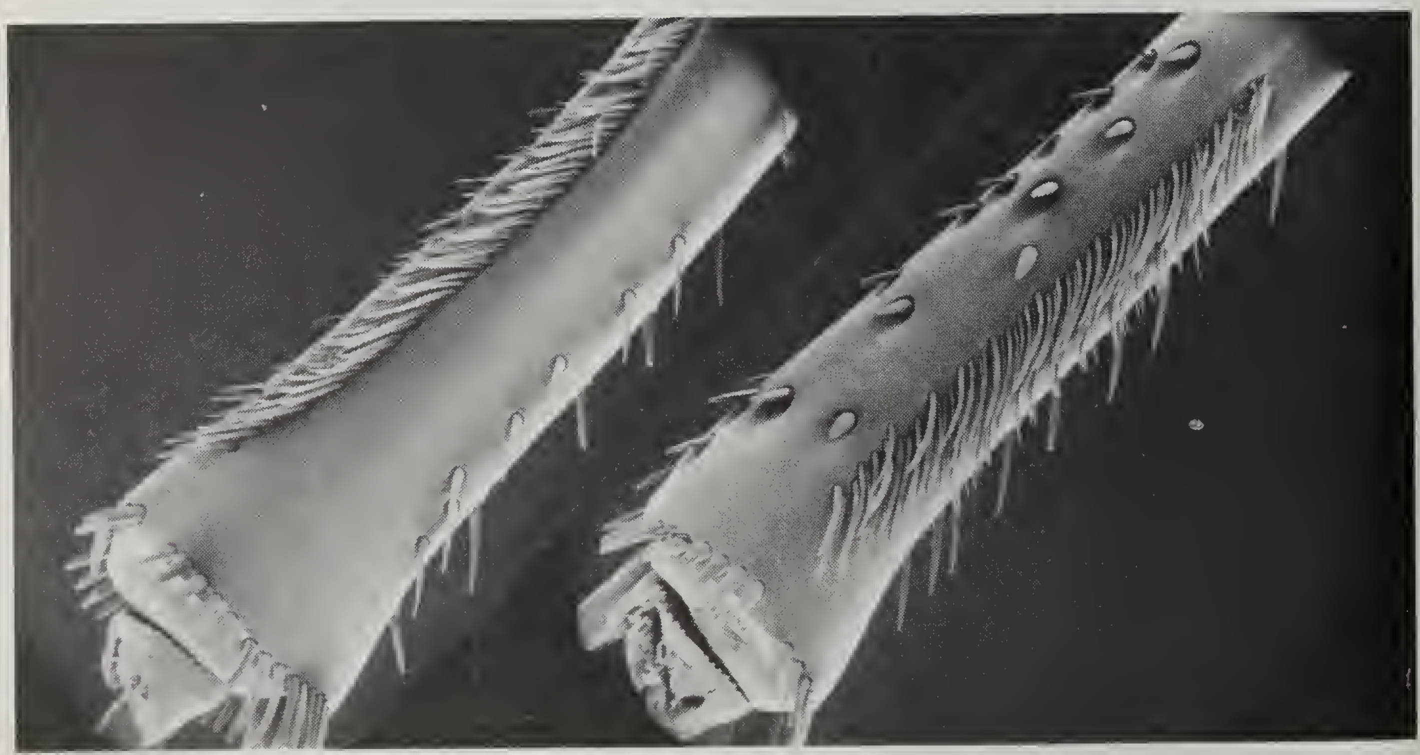

Fig. 3. *Enceladus gigas* adult mesotibial brush, oblique lateral view, Trinidad.

There is little doubt that *Cymbionotum,* regarded by Andrewes (1935) as constituting its own tribe, is closely related to *Siagona.* They share the following apotypic states: 1) sulcate neck, 2) pubescent antennomeres 1-4, 3) pilose body surface, 4) depressed form, 5) one supraorbital seta, and 6) clavate scape. States 4, 5, 6 are also shared with *Luperca,* regarded here as the sister group to the first mentioned two. All three of these can be regarded as the sister group of *Enceladus* by virtue of larval character states (see above) and the mesotibial brush, expanded supramaxillary plate, pedunculate body, and entire scutellar stria. Our present state of knowledge of the distribution of these last 4 states leaves much to be desired and only the supramaxillary plate expansion can definitely be regarded as apotypic. However, the hypothetical ancestor or so-called stem species of Siagoninae can be characterized as having had a well developed mesotibial brush, pedunculate form, expanded supramaxillary plate, entire sutural stria and notched clypeus. Its body form was that of a small *Enceladus* or *Pasimachus.* The parameres were fringed with setae and the spurs of the front tibiae were terminal or nearly so.

The group of 4 genera discussed above and here regarded as constituting the tribes Enceladini (*Enceladus)* and Siagonini (*Luperca, Cymbionotum,* and *Siagona)* in the subfamily Siagoninae are predominantly found in the Old World tropics. Table I provides distribution summaries for each genus. The patterns of distribution found for extant species indicate the group as a whole is an old one; relicts are of higher taxonomic levels for the most part (*Enceladus, Luperca).* Recent radiation perhaps has occurred in *Siagona* and *Cymbionotum* for they are all widespread, lowland, highly vagile dispersants. The New World/Old World tribal separation of Enceladini/Siagonini probably arose before Africa and South America rifted apart. Enceladini occupied more or less its present range at that time; rifting gave it complete isolation from the rest of the group. The Siagonini occupied the eastern portions of Gondwana, and rifting kept them from invading the New World.

This hypothetical scenario can be tested and potentially found false by: 1) discovery of fossils of groups outside the ranges described above; 2) additional character suites could be analysed to test the proposed relationships; and finally, 3) the discovery of the sister group of Siagoninae might place its origin elsewhere than Gondwana tropics. Likely candidates for

Fig. 4. *Melaenus elegans* adult mesotibial oblique comb, oblique lateral view, Tabalpun, India.

this sister group are the Scaritini or Broscini. No broscines I studied had a mesotibial brush, but the scaritine *Pasimachus* has a row of closely packed setae which may be the precursor to the Siagoninae brush. Thus, the similar forms of *Enceladus* and *Pasimachus* may not be convergence.

The zoogeographic scenario presented above rests on the assumption that correct phylogenetic interpretations have been made. Unfortunately many groups require analysis, and further testing must be done with unstudied character states.

Classification

In order not to upset the presently used classification of Carabidae based on the small selection of tribes here studied, I have continued to use, for the most part, tribes currently in use or in use in the past. Only Cymbionotini has been synonymized with Siagonini. Subfamilial ranking in Carabidae is due for a total overhaul soon.

Melaenus was placed with Siagonini by de La Porte (1834), and Jeannel (1946) thought the Promecognathini were part of the "Siagonidae." These actions do not fit the present data. Kryzhanovskij (1976) correctly aligned Cymbionotini with Siagonini and Enceladini. Apotomini was given subfamily rank by Britton (1970) but if relationships with Elaphrini, Promecognathini, Melaenini, Loricerini, and Migadopini are shown to be correct this action may have been premature.

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